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Biodiversity, Biogeography, and Conservation of Bats in the Lesser Antilles

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Biodiversity, Biogeography, & Conservation of Bats in the Lesser Antilles

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The chiropteran fauna of the Lesser Antilles consists of 27 species. The diversity of this fauna is low when compared with Neotropical faunas of large continental islands or at sites on the adjacent mainland, however, the Lesser Antillean fauna contains 11 species endemic to these islands making it worthy of large-scale conservation efforts. At the southern end of the Lesser Antilles, the biological limit of the Lesser Antillean bat fauna is marked by Koopman's Line. To the south of this line, the bat faunas of the Grenadines and Grenada are composed of South American and widespread species of bats. The central Lesser Antillean islands have been grouped as the "Lesser Antillean Faunal Core." The bat faunas of these islands are characterized by the presence of 9 or more species and several endemic species that occur on only one or two of these islands. The faunas of the northern Lesser Antillean islands are united into the "Northern Antillean Faunal Area" and share the same eight species of bats. The conservation of bats is critical not only to the biodiversity that they represent, but to the maintenance of biodiversity of other fauna and flora. The maintenance of chiropteran fauna can best be served by three actions—preservation of caves, preservation of forest diversity, and restoration of hydrological systems.

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À l'initiative de Jean-Louis VERNIER

Direction de l'Environnement, de l'Aménagement et du Logement de la Martinique

Sous la direction de Maurice BURAC

Professeur émérite, GÉODE-AIHP, Université des Antilles et de la Guyane

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Taxonomic Diversity in the Lesser Antilles

The chiropteran fauna of the Lesser Antilles consists of 27 species of bats representing 7 families (Table 1). The diversity of this fauna is low when compared with Neotropical faunas of large continental islands or sites on the adjacent mainland—Suriname (95 species), Nicaragua (85), Trinidad (64), Yucatan Peninsula (48), and coastal Venezuela (39) (Genoways *et al.*, 2001). The Lesser Antillean bat fauna contains 11 species that are endemic to these islands and a 12th species—*Brachyphylla cavernarum*—that is endemic to the Antilles (Table 1). This represents a significant amount of biodiversity and is worthy of large-scale conservation efforts. These species of bats are not uniformly distributed throughout the Lesser Antilles, but occur in patterns that provide insight into the development of the bat faunas of these islands (Table 2).

Table 1: List of the species of bats occurring on the Lesser Antillean islands.

Family Emballonuridae	
<i>Peropteryx trinitatis</i>	
Family Mormoopidae	
<i>Pteronotus davyi</i>	
<i>Pteronotus rubiginosus</i>	
Family Noctilionidae	
<i>Noctilio leporinus</i>	
Family Phyllostomidae	
<i>Brachyphylla cavernarum</i>	*
<i>Anoura geoffroyi</i>	
<i>Glossophaga longirostris</i>	
<i>Monophyllus plethodon</i>	**
<i>Micronycteris buriri</i>	**
<i>Micronycteris megalotis</i>	
<i>Ardops nichollsi</i>	**
<i>Dermanura bogotensis</i>	
<i>Artibeus jamaicensis</i>	
<i>Artibeus lituratus</i>	
<i>Artibeus planirostris</i>	
<i>Artibeus schwartzi</i>	**
<i>Chiroderma improvisum</i>	**
<i>Sturnira lilium</i>	
<i>Sturnira thomasi</i>	**
Family Vespertilionidae	
<i>Eptesicus fuscus</i>	
<i>Eptesicus guadeloupensis</i>	**
<i>Myotis dominicensis</i>	**
<i>Myotis martiniquensis</i>	**
<i>Myotis nyctor</i>	**
Family Natalidae	
<i>Natalus stramineus</i>	**
Family Molossidae	
<i>Molossus molossus</i>	
<i>Tadarida brasiliensis</i>	

* Restricted in distribution to the Lesser Antilles, Virgin Islands, and Puerto Rico.

** Endemic to the Lesser Antilles.

Table 2. Chiropteran species inventories for the Lesser Antilles. Species endemic to the Antilles are in bold and islands are arranged (approximately) from north to south. Solid circles show documentation of species by voucher specimens and/or genetic data. Asterisks indicate hybridization (H) among southern Lesser Antillean populations of *Artibeus jamaicensis*, *A. planirostris*, and *A. schwartzi*. Dashed lines define the Northern Antillean Faunal Area (Anguilla–Antigua) and Lesser Antillean Faunal Core (Montserrat–St. Vincent). Solid line identifies the southern Lesser Antillean location of Koopman's Line (east and south of Barbados westward through the Bequia Channel).

	Anguilla	St. Martin	St. Barthélemy	Saba	St. Eustatius	St. Kitts	Nevis	Barbuda	Antigua	Montserrat	Guadeloupe	Dominica	Martinique	St. Lucia	St. Vincent	Barbados	Grenadines	Grenada
<i>Ardops nichollsi</i>			•	•	•	•	•	•	•	•	•	•	•	•				
<i>Artibeus schwartzi</i>*													H	•	H	•	H	
<i>Brachyphylla cavernarum</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		
<i>Chiroderma improvisum</i>										•	•							
<i>Eptesicus guadeloupensis</i>											•							
<i>Micronycteris buriri</i>														•				
<i>Monophyllus plethodon</i>	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•		
<i>Myotis dominicensis</i>												•						
<i>Myotis martiniquensis</i>											•	•	•		•			
<i>Myotis nyctor</i>															•			•
<i>Natalus stramineus</i>	•	•		•			•	•	•	•	•	•	•					
<i>Sturnira thomasi</i>										•	•							
<i>Anoura geoffroyi</i>																		•
<i>Artibeus jamaicensis</i> *	•	•	•	•	•	•	•	•	•	•	•	•	H		H	H		
<i>Artibeus lituratus</i>														•		•	•	
<i>Artibeus planirostris</i> *															H	H		•
<i>Carollia perspicillata</i>																		•
<i>Dermanura bogotensis</i>																		•
<i>Eptesicus fuscus</i>											•	•						
<i>Glossophaga longirostris</i>														•		•	•	
<i>Micronycteris megalotis</i>																		•
<i>Molossus molossus</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Noctilio leporinus</i>		•				•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Peropteryx trinitatus</i>																		•
<i>Pteronotus davyi</i>											•	•	•	•				•
<i>Pteronotus rubiginosus</i>															•			
<i>Sturnira lilium</i>												•	•	•	•			•
<i>Tadarida brasiliensis</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			

The Lesser Antilles chain is defined geologically by the Anegada Passage in the north and the southern end of the Grenada Bank in the south. When looking at the modern chiropteran fauna, the Anegada Passage would seem to be a zoogeographic barrier, but when the fossil evidence of the last 10,000 years is considered, this passage is less of a barrier (Genoways *et al.*, 2007c). At the southern end of the Lesser Antilles, the biological limit of the Lesser Antillean bat fauna is marked by Koopman's Line, which passes through the Bequia Channel just south of St. Vincent (Figs. 1 and 2). South of this line (with the possible exception of *Artibeus schwartzi*), the bat faunas of the Grenadines and Grenada are composed of South American and widespread species of bats. These faunas can be classified as attenuated South American faunas (Genoways *et al.*, 1998; Genoways *et al.*, 2010). The chiropteran faunas of Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, and St. Vincent have

been grouped as the “Lesser Antillean Faunal Core” and are characterized by the presence of nine or more species and several endemic species that occur on only one or two islands (Genoways *et al.*, 2001). The faunas of the islands of Anguilla, Antigua, Barbuda, Nevis, Saba, St. Barthélemy, St. Eustatius, St. Kitts, and St. Martin have been united into the “Northern Antillean Faunal Area.” These island faunas share the same eight species of bats (Genoways *et al.*, 2007a). This faunal area can be seen as a transition zone between the Lesser Antillean Faunal Core and the Greater Antillean Faunal Core, which includes the bat fauna of Cuba, Hispaniola, Jamaica, and Puerto Rico. Barbados, at the southern end of the Lesser Antilles, has been in existence for only 1 million years or less (Speed and Keller 1993), yet has been colonized and populated within this short period of time.



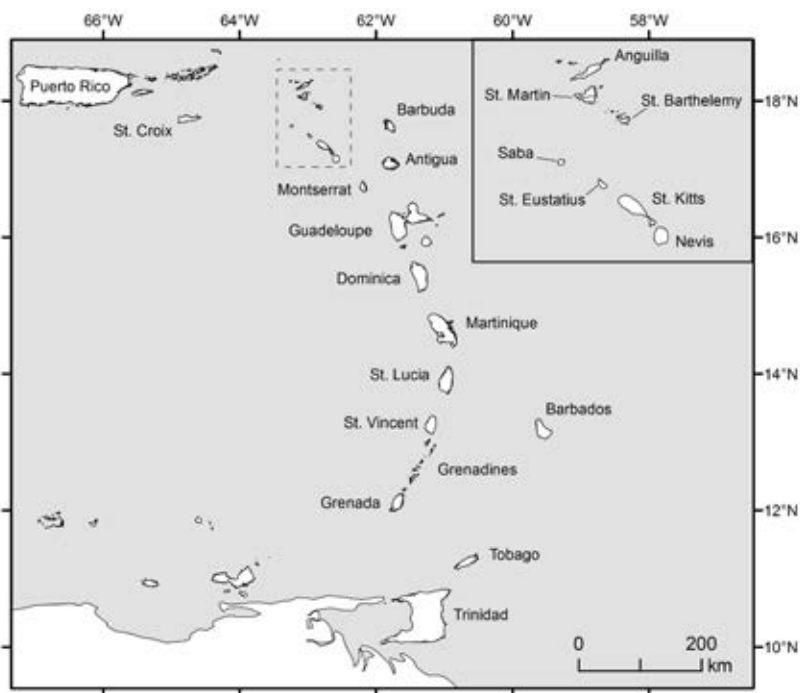


Figure 1. Map of the eastern Caribbean and the Lesser Antilles

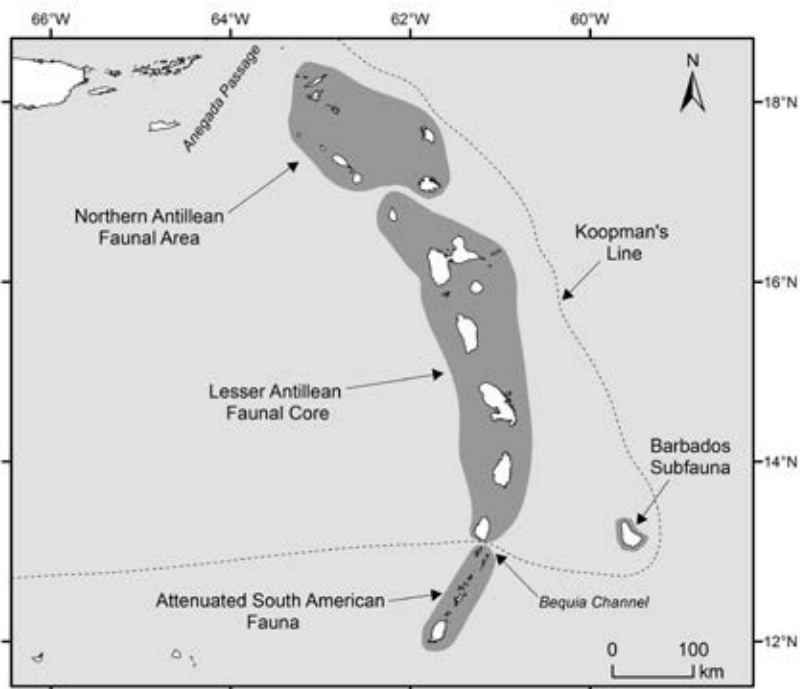


Figure 2. Map indicating the Northern Antilles Faunal Area, the Lesser Antilles Faunal Core, and Koopman's Line

Limitations On and the Complexity of Biodiversity Data

Before we can make broad statements about bat biodiversity and bat conservation, we must first re-visit the limitations and bias under which our data were collected.

Net Bias—Accurate species inventories for an island are hampered by the inadequacy of ground-based netting strategies, something that has been painfully obvious to field biologists who study species-specific responses to mist nets and species-specific ability to avoid mist nets (Barber *et al.*, 2003; Berry *et al.*, 2004; Lang *et al.*, 2004; R. Larsen *et al.*, 2005, 2006, 2007; Simmons and Voss, 1998). Species that are not captured in surveys on a regular basis may simply be able to avoid mist nets, or fly where we cannot place mist nets, or are quite simply rare. Given this difficulty in accurately quantifying bat abundance and diversity, we have used a simple metric (bats per net-night: BNN) to approximate activity levels at our sampling sites on various islands throughout the region (Genoways *et al.*, 2007a, 2007b, 2007c; P. Larsen *et al.*, 2007; R. Larsen *et al.*, 2005, 2006, 2007; Pedersen *et al.*, 1996, 2003, 2005, 2006, 2007). The addition of other variables (e.g., net dimensions, net-hours, etc.) introduces false precision to the data and thereby increases bias in the survey data. BNN would seem therefore to be the most pragmatic metric with which to cross-evaluate historical data from numerous investigators and sampling protocols (Fenton *et al.*, 1992; LaVal, 2004; Pedersen *et al.*, 2005).

Survey Duration—Our efforts have shown that short-duration and/or single season surveys underestimate bat biodiversity; the capture of rare species requires a greater investment of time and effort. We conclude that without long-duration/multi-year survey efforts, biodiversity estimates can only be approximations at best and quite probably underestimate the true faunal diversity of an island, thus providing a poor foundation for any subsequent conservation guidelines.

Survey Timing: Disturbance, Sex, and Time Frame—The severity and frequency of environmental disturbance has considerable influence on biodiversity in the eastern Caribbean. What appears to the human eye as a natural disaster, may be perceived by the biota on any one of these hurricane-dominated volcanic islands as perfectly "normal," evolutionarily speaking. Indeed,



despite the great fluctuations in bat abundance on Montserrat over the last 30 years, none of the 10 species of bats has been extirpated despite dramatic volcanic activity and a Category 5 hurricane (Pedersen *et al.*, 2009). During that time, some of our surveys yielded only 4 species of bat, and *Chiroderma* and *Sturnira* were not found from 1994 to 2004 despite extensive efforts. Had some of these species been extirpated by storms/volcanic activity and then subsequently re-colonized the island, or had they simply become so rare as to have become "invisible" to our mist netting efforts (R. Larsen *et al.*, 2005, 2007)?

Fenton *et al.*, (1992) demonstrated that phyllostomid bats are indicators of habitat disruption, and island populations of fruit bats appear more susceptible to habitat disruption than are mainland populations (Barlow *et al.*, 2000). However, many bats in the Lesser Antilles seem to be disturbance adapted. Unlike their mainland congeners, these animals and their reproductive strategies have evolved in a region dominated by natural disasters. The low reproductive rates of most chiropteran taxa ("k-selected" organisms) are poorly suited for responding rapidly to disturbance in these complex, inherently unstable, tropical communities. Interestingly, *Artibeus* would seem to be capable of alternating between k- and r-selected reproductive strategies (Kwiecinski and Pedersen, 2002), whereas other fruit bats (*Monophyllus*, *Aradops*, or *Brachyphylla*) are not. Our data suggest that *Artibeus* recovers quickly after a drought or a natural disaster, and can become numerically dominant on small islands. This is an interesting observation that bears further investigation—to what extent does reproductive strategy account for the contemporary community structure of bats throughout the Lesser Antilles?

So "when" do we perform a species inventory/biodiversity survey on any one of these islands? What is the appropriate slice of time that should be used when constructing species-area curves? When was the most recent disturbance? Should human development/impact be factored-in? Assuming that time might ameliorate stochastic events, should fossil data be included in an island's fauna (Pedersen *et al.*, 2006; Steadman *et al.*,

1984a, 1984b)? Is there a disturbance frequency/severity threshold for bat extirpation, or could it be that we must wrestle with a complicated and resilient metapopulation of bats throughout the Lesser Antilles?

Bat Biodiversity: Species-Area Curves—The number of species found on an island is correlated with the size (area) of the island, the distance from a source area (continental area) and the diversity of habitats available, which in most cases is directly affected by elevation of the island (MacArthur and Wilson, 1967). When looking at species-area curves for mammals, birds, lizards, and insects throughout the Caribbean, z-values (slope of the regression line) range from 0.48 to 0.20, with highly vagile species exhibiting low z-values (Davies and Smith, 1998; Griffiths and Klingener, 1988; Morgan and Woods, 1986; Wilcox, 1980). Low z-values

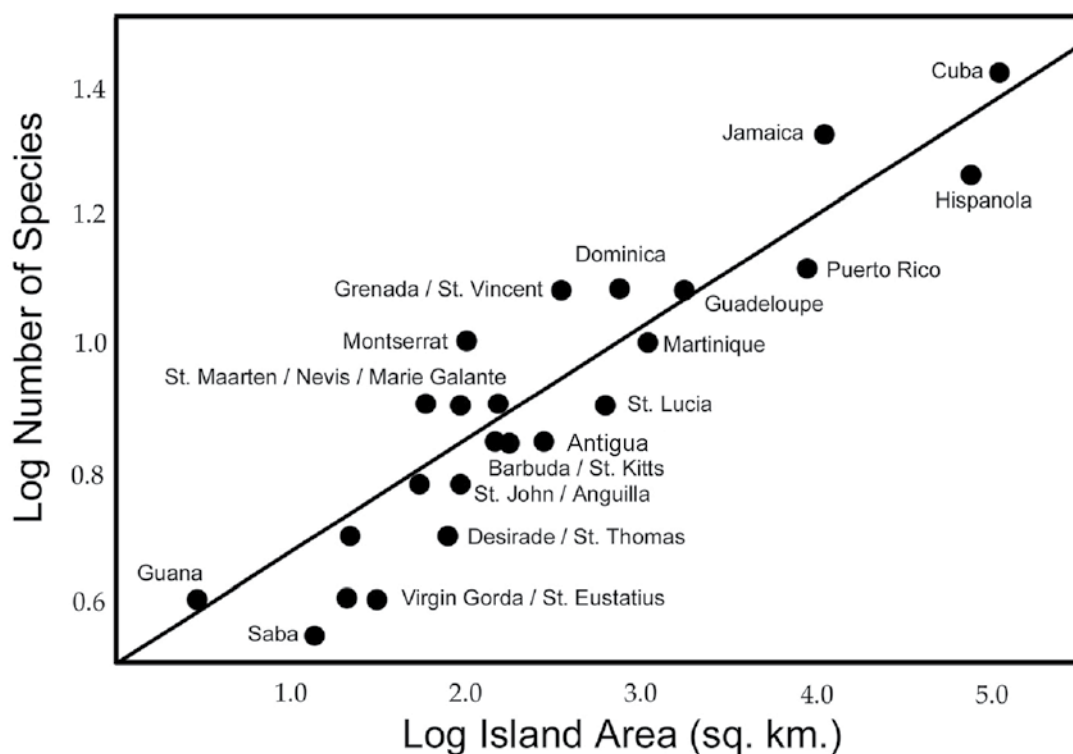



Figure 3. Species area curve for Lesser and Greater Antillean bat faunas (after Pedersen *et al.*, 2009). Linear regression of log-transformed data: $y = 0.17x + 0.49$ ($R^2 = 0.81$).

suggest a greater propensity for dispersal or a reduced extinction rate relative to other West Indian biota (Davies and Smith, 1998). Not surprisingly, our z-value of 0.17 for bats is very low (Pedersen *et al.*, 2009; Fig. 3). We have also included fossil data, island elevation, and the treatment of different feeding guilds separately in our models, which has been productive in some cases (Pedersen *et al.*, 2005, 2006). Certainly, island elevation ameliorates the effect of small surface area on very small islands such as Saba (Genoways *et al.*, 2007a).





From the perspective of bat conservation, the relative position of an island above or below the “curve” is of great importance. Islands with relatively high levels of bat diversity appear above the line and can be attributed to (1) sufficient/diverse natural habitat; (2) close proximity to a source island; or (3) extensive biodiversity survey efforts.

The position of an island below the “curve” may be attributed to (1) a dearth of habitat and/or habitat diversity due to island geology, history of natural disasters, or the impact of human activity; (2) the presence of a biological barrier that is difficult for bats to surmount; (3) a simple case of under-sampling due to a variety of reasons (Pedersen *et al.*, 2003), or even because (4) the demographics/natural history of each species is different and some species have yet to colonize the island (e.g., “old” invasions by *Myotis* and “recent” invasions like *Artibeus*).

Recent literature encourages the use of a new paradigm of island biogeography (Brown and Lomolino, 2000; Heaney, 2007; Lomolino, 2000a, b; Whittaker, 2000). Lomolino (2000a) and Brown and Lomolino (2000) list 3 limitations of equilibrium theory as species diversity (1) is not and may never be at equilibrium, (2) is shaped by variation in speciation, colonization, and extinction among taxa, and (3) is changed by differences among islands beyond area and isolation alone. With a better understanding of the complexity of the scales of nature (i.e. spatial, temporal, and ecological; Lomolino, 2000a; Whittaker, 2000), variables beyond the balance of immigration and extinction in island systems must be considered. Several alternatives and modifications to MacArthur and Wilson’s (1967) equilibrium theory of island biogeography have been suggested within the last decade (see Lomolino 2000b – hierarchical species-based model) and include the addition of more complex variables (including evolution) into the simplistic equilibrium model (Lomolino, 2000a; Whittaker, 2000). Removing evolution from the original model allowed MacArthur and Wilson (1967) to assume variation in species richness was controlled by area and isolation alone, and species abilities to colonize and propagate different islands were equivalent (Lomolino, 2000a). Additionally, Heaney (2007) comments on several of the aspects of a new paradigm, which include frequency of dispersal, variation in gene flow, factors affecting species diversification, correlation of island age and inhabiting species’ ages, species persistence on islands, and re-colonization of continents by island species.

Dispersal patterns in the Lesser Antilles—Terrestrial vertebrate movement along archipelagoes is thought to happen primarily by accidental rafting events (Censky *et al.*, 1998; Raxworthy *et al.*, 2002; Schoener *et al.*, 2001). For birds and bats, the question of dispersal is more complex because they are capable of flight (Fleming and Murray, 2009;


Koopman, 1977; Whittaker, 1998). Pumo *et al.* (1996) and Carstens *et al.* (2004) imply restricted dispersal ability among the islands for the cave-roosting endemic, *B. cavernarum*, resulting in isolated intra-island gene pools, whereas the Caribbean eurytopic *A. jamaicensis* showed little isolation and apparently moves among the islands more often. As these genetic data imply, and with the possible exception of *Noctilio leporinus*, Antillean bat species do not voluntarily move over water from one island to another on a regular basis (see also Fleming and Murray, 2009). Based on the available data, we conclude that tropical storms, not bat behavior, are responsible for insular dispersal and gene flow for bat populations living in the Lesser Antilles.

Genetic-Level Diversity and Phylogeographic Patterns

What follows is a brief review of recent studies of the molecular systematics and phylogeography of Lesser Antillean bats (*Table 2*).

Emballonuridae.—The Lesser Antillean representative of this family, *Peropteryx trinitatis phaea* (sensu Simmons, 2005) from Grenada, has not been examined genetically. Lim *et al.* (2008) included specimens of *P. trinitatis* collected from northern South America and Trinidad in their analysis of New World Emballonurid bats. Their data show that *P. trinitatus* is genetically distinct from *P. macrotis*, therefore providing further evidence that *P. trinitatis* is a taxonomically valid species (see Brosset and Charles-Dominique, 1990). A detailed genetic analysis of specimens from Grenada, Trinidad, and Tobago is clearly warranted based on the observations by Genoways *et al.* (1998) regarding the morphological variability exhibited throughout this region.

Mormoopidae.—Lewis-Oritt *et al.* (2001a) and Davalos (2006) examined phylogenetic variation in both mitochondrial and nuclear DNA datasets from several species of *Pteronotus*. Davalos (2006) elevated the subspecies *P. parnellii rubiginosus* to species status and our molecular identifications of specimens from St. Vincent are congruent with this taxonomic arrangement. Thus, *P. rubiginosus* is the appropriate binomial for Lesser Antillean populations formally identified as *P. parnellii* on St. Vincent. Moreover, our analyses indicate a close relationship between St. Vincent and Suriname populations of *P. rubiginosus* (< 1% in cytochrome-b gene variation). This indicates colonization of the Lesser Antilles from northern South America by *P. rubiginosus*. Davalos (2006) also examined genetic variation within *Pteronotus davyi* and included specimens collected from Dominica in her analyses. The results of Davalos (2006) indicate a close relationship between *Pteronotus davyi* on Dominica and Trinidad, also indicating a northern South American origin for Lesser Antillean populations of this species.



Noctilionidae.—Lesser Antillean populations of *Noctilio leporinus* exhibit low (< 1.5%) mitochondrial DNA sequence variation across their distribution (Lewis-Oritt *et al.*, 2001b). This result indicates a fairly recent colonization of the Lesser Antilles by this species, most likely originating from northern South America. Moreover, the genetic data indicate multiple colonization events by *N. leporinus* into the Lesser Antilles (see Genoways *et al.*, 2010).

Phyllostomidae.—Of the Lesser Antillean representatives of the family Phyllostomidae, the most detailed phylogenetic analyses have been performed on the genus *Artibeus* (P. Larsen *et al.*, 2007; P. Larsen *et al.*, 2010; Phillips *et al.*, 1989; Phillips *et al.*, 1991; Pumo *et al.*, 1996). Collectively the data from *Artibeus* indicate recent (late Pleistocene/Holocene) colonization events by *A. jamaicensis* from Central America and *A. planirostris* and *A. lituratus* from northern South America (Genoways *et al.*, 2005; Genoways *et al.*, 2010; P. Larsen *et al.*, 2007; P. Larsen *et al.*, 2010). Perhaps the most interesting aspect of the genetic variation present in Lesser Antillean populations of *Artibeus* is found with the endemic *A. schwartzi*. Mitochondrial, nuclear, and morphological data indicate that contemporary populations of *A. schwartzi* on St. Vincent and throughout the Grenadines are the product of extensive hybridization among multiple species of *Artibeus* (see P. Larsen *et al.*, 2010). The potential hybrid origin for *A. schwartzi* and evolutionary significance of hybridization among multiple lineages of *Artibeus* is discussed in detail by P. Larsen *et al.* (2010). It should also be noted that the hybrid zone within Lesser Antillean populations of *Artibeus* coincides with the geographic position of Koopman's Line (Genoways *et al.*, 2010).

Relatively few studies have examined the patterns of genetic variation within the Lesser Antillean endemics *Brachyphylla cavernarum*, *Ardops nichollsi*, *Monophyllus plethodon*, *Chiroderma improvisum*, and *Sturnira thomasi*. Carstens *et al.* (2004), Davalos (2004), and Murray (2008) did examine genetic variation within *B. cavernarum*. Their results indicate (1) a close genetic relationship between *B. cavernarum* and *B. pumila* (< 3% in cytochrome-b gene sequence data), and (2) a recent expansion by *B. cavernarum* throughout the Lesser Antilles. The population genetic structure and molecular systematics of *Ardops nichollsi* has been investigated by Carstens *et al.* (2004), Davalos (2004), and Davalos (2007). Collectively the data from these studies indicate low sequence variation within *Ardops nichollsi* and a close genetic relationship between *Ardops* and *Arriteus*. These results are consistent with the hypothesis of a relatively recent origin (~ 2 million years ago) of the genus *Ardops* (Baker *et al.*, 2012). Baker *et al.* (1994) used cytochrome-b sequence data to examine interspecific relationships within the genus *Chiroderma*. This molecular marker inferred a sister relationship between *C. improvisum* and *C. villosum* (distributed in Central and South America), whereas the most

basal species in the genus, *C. salvini*, is found throughout Middle, Central and South America. This may indicate the ancestor of the Lesser Antillean lineage originated from Central or South America. Additional studies of *M. plethodon* and *S. thomasi* are ongoing.

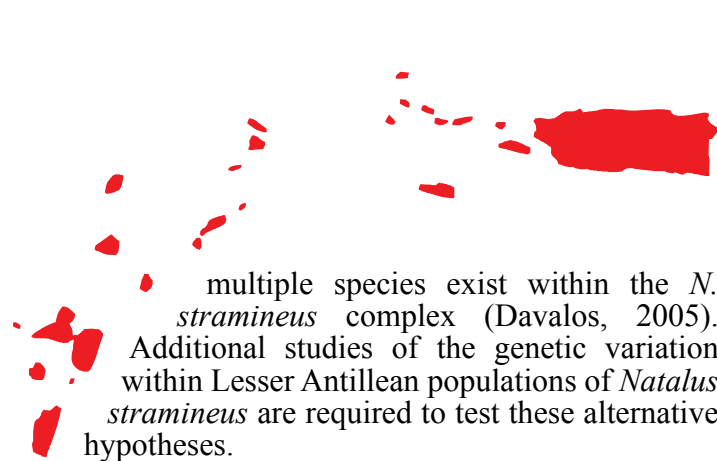
Phylogenetic analyses indicate that *M. buriri* is within the subgenus *Micronycteris* and is most closely related to specimens referable to *M. megalotis*. The cytochrome-b gene genetic distance values separate *M. buriri* from mainland members of the *M. megalotis* complex range from 1.9% (*M. buriri* versus Tobago *M. megalotis*) to 6.0% (*M. buriri* versus Suriname *M. megalotis*) (P. Larsen *et al.*, 2011).

Genetic data from *Glossophaga longirostris* (Hoffmann and Baker, 2001) indicate a close relationship among populations distributed from St. Vincent southward to Trinidad and Tobago, thus suggesting a colonization of the southern Lesser Antilles from northern South America. Robust genetic analyses of the remaining Lesser Antillean phyllostomids *Anoura geoffroyi*, *Dermanura bogotensis*, *Micronycteris megalotis*, and *Sturnira lilium*, are either absent or ongoing.

Vespertilionidae.—Ruedi and Mayer (2001) and Stadelmann *et al.*, (2007) included the Lesser Antillean endemics *Myotis dominicensis* and *M. martiniquensis* in their analyses of New World species of *Myotis*. Collectively, their data show a sister relationship between *M. dominicensis* and *M. martiniquensis*. However, these existing molecular datasets fail to elucidate the biogeographic origins of the Caribbean populations of *Myotis*. This failure is attributable to saturation of molecular markers and/or poor taxonomic sampling throughout Central and South America. Previous authors (using morphological data) have suggested the origins of Lesser Antillean *Myotis* are from South America (Baker and Genoways, 1978; LaVal, 1973; LaVal and Schwartz, 1974). A recent study by R. Larsen *et al.* (2012) indicates that the subspecies *M. m. nyctor* from Barbados is genetically and morphologically distinct from *M. martiniquensis*, warranting recognition of a third Caribbean endemic, which is most closely related to a population from Grenada.

Natalidae.—Davalos (2005) included specimens of *Natalus stramineus* collected from Dominica and Marie Galante in her examination of the genetic variation within Natalidae. Her results show that the mitochondrial lineages (cytochrome-b gene sequence data) within *N. stramineus* are paraphyletic with respect to *N. tumidirostris* from Trinidad. Several hypotheses could account for this result and include, (1) incomplete lineage sorting, (2) mitochondrial introgression subsequent to hybridization, or (3)






multiple species exist within the *N. stramineus* complex (Davalos, 2005). Additional studies of the genetic variation within Lesser Antillean populations of *Natalus stramineus* are required to test these alternative hypotheses.

Molossidae.—Phylogenetic analyses using molecular data from Lesser Antillean populations referable to *Molossus molossus* and *Tadarida brasiliensis* remain to be conducted. Genoways *et al.* (1981) and Timm and Genoways (2003) identified significant morphological variability among Antillean populations of *M. molossus* indicating that the species complex was in need of taxonomic revision. With respect to *T. brasiliensis*, there are subtle morphological differences that separate the subspecies *T. b. antillularum* and *T. b. constanzae* (Timm and Genoways, 2003). However, the significance of this variation remains to be determined and requires a taxonomic assessment of the entire *Tadarida brasiliensis* complex using molecular data.

Bat Conservation Issues in the Lesser Antilles

The conservation of bats is not only important to maintain their contribution to island biodiversity, but because they are linked to the maintenance of other aspects of the region's fauna and flora. The maintenance of chiropteran fauna can best be served by three conservation actions treated separately below—preservation of caves, preservation of forests, and restoration of hydrological systems.

Preservation/Protection of Caves—At least 10 species of bats occurring in the Lesser Antilles are obligate cave roosters, or will roost in rock fissures/overhangs if caves are not available. Caves and their man-made equivalents (mines, wells, cisterns, abandoned buildings) provide critical refugia in times of natural disaster (Gannon and Willig, 1994; Pedersen *et al.*, 1996), and are one of the most critical limiting factors for several bat species (Genoways *et al.*, 2007a, 2007b, 2007c; Pedersen *et al.*, 2003, 2005, 2006). Conversely, cave roosts pose a risk to their occupants if the cave is destroyed suddenly (e.g., earthquakes, volcanic activity, human action; Genoways *et al.*, 2007b). Our observations indicate that most caves throughout the region are heavily impacted by human activities (vandalism, used as garbage dumps, buried beneath housing developments and roads, used as housing for livestock, and even modified for human habitation).



Conservation efforts often underestimate or even ignore the fragility of cave systems and the valuable hidden levels of biodiversity therein. Guano


produced by cave roosting bats is the primary energy source for entire ecosystems of obligate cave vertebrates, invertebrates, plants, and fungi. The protection of caves should be a priority for any island conservation effort.

Preservation/Protection of Forests—Several bat species utilize caves in a facultative manner, but more commonly roost in the cavities of large trees (living or dead), or in foliage roosts such as beards of several types of palm-tree. Foliage roosts pose a very different kind of conservation problem that involves the protection of forests. Healthy forests require healthy bat populations and healthy bat populations require healthy forests. Forests provide roosts, protection, and food resources for bats, in return, bats provide several vital functions for the forests, including insect control, pollination of a wide-variety of plant species, and the subsequent dispersal of plant seeds.

The 12 species of insectivorous bats occurring in the Lesser Antilles consume a wide variety of nocturnal insects and help control these insect populations. The nutrients represented by these insects are transported by insectivorous bats from the foraging areas back to their roosting sites thus contributing to the cycling of energy and nutrients through forest and cave ecosystems (Jones *et al.*, 2009).

More than 350 species of plant representing 44 plant families are bat-pollinated (Fleming *et al.*, 2009); bats play a vital role in maintaining the genetic diversity in tropical plant communities (Fleming *et al.*, 2009; Quesada *et al.*, 2004). Bat-pollinated plants include large tropical forest trees, such as kapok (*Ceiba pentandra*), sandbox tree (*Hura crepitans*), and royal palm (*Roystonea regia*), to cactus (*Neobuxbaumia euphorbioides*), and agave (*Agave angustifolia*) (Fleming *et al.*, 2009). Native fruit trees, such as guava (*Psidium guajava*) and the introduced banana (*Musa paradisiaca*) also are pollinated by bats (Soto-Centeno and Kurta, 2006). Bats do not specialize in pollinating a single species of plant, but visit a range of species available in their habitat (Heithaus *et al.*, 1975; Muchhala and Jarrín-V., 2002; Nassar *et al.*, 2003; Soto-Centeno and Kurta, 2006; Tschapka *et al.*, 2008; Quesada *et al.*, 2004). Bats are excellent pollinators because they readily overcome distances between various plants and carry heavier pollen loads than other pollinators (e.g., insects, birds).

The 15 species of phyllostomid bats occurring in the Lesser Antilles are involved in the pollination and seed dispersal of some ecologically and economically important plant species (Howe and Miriti, 2004; Jones *et al.*, 2009). Bats frequently disperse seeds of pioneer plants (e.g., *Cecropia*, *Solanum*, *Piper*) critical to the revegetation of areas that had been cleared for agriculture or that have been heavily damaged by hurricanes or volcanic eruptions (Jones *et al.*, 2009; Kelm *et al.*, 2008; Martínez-Garza and González-Montagut, 2002; Medellín and



Gaona, 1999). Although birds have long been credited as seed dispersers, Medellín and Gaona (1999) found that bats account for more than half of the "seed rain" in a variety of tropical forest habitats in southern Mexico.

Protection and Restoration of Hydrological Systems—Perhaps most importantly, healthy forests are vital to the maintenance of an island's hydrologic system of small streams, aquatic habitats, soil moisture levels, the humidity of numerous microhabitats and ecological niches, and all of the biodiversity that these represent.

Many hydrological systems throughout the Lesser Antilles have been dramatically altered for human consumption and irrigation of crops, sometimes with great damage to the entire ecosystem (Genoways *et al.*, 2007b). Protection of fresh water resources is imperative for any and all conservation efforts. Real estate development and road construction must be done more carefully with consideration for deforestation and water runoff. If sedimentation is reduced, we can limit damage to natural springs and natural hydrological cycles. Healthy hydrologic systems help insure clean water resources and this benefits forests, wildlife, and the human populations on these islands.

Our use of molecular-based studies adds to the previous faunal and ecological surveys (at various time frames and in variable environmental conditions and habitats) by increasing our understanding of the genetic variation in the bat fauna of the Lesser Antilles, in light of a modern theory of island biogeography. This broadens our understanding of the complex patterns and processes influencing island systems and island biota.

The conservation needs of bats are relatively straightforward; their foraging areas and roost sites must be preserved. Where possible, forests should be protected. This could be accomplished in several ways: land purchase by local governments/NGOs, or by reforestation programs as part of a wildlife management option. Forests could also be preserved by establishing wildlife management zones according to areas of conservation priority, species priority, land-ownership, etc. Where possible forest enrichment could be achieved by planting native species and forest habitat could be enhanced by creating corridors between forest fragments. Where possible, water resources should be maintained or restored to support plant and animal communities that are not only vital to the health of bats and forests, but to that of humans as well. Roost sites such as caves must also be protected but deep sheltered ravines on some of the more mountainous islands also provide significant roosting options and refuge during large storms. Perhaps deep ravines and caves should be viewed as ecological equivalents from both evolutionary and animal conservation perspectives.

There is a tremendous need to increase awareness and to educate the public about local bats. Without public involvement in conservation, bat populations and everything that relies on them will suffer. Awareness and education can be accomplished by creating displays and information kiosks at local festivals and agricultural fairs. Wildlife management agencies can work with local schools to develop youth-based conservation programs for native species and sustainable development. Simple information booklets can be printed and distributed to encourage the planting of native fruit trees on both public and private lands that will in turn support a wide range of native bird and bat species.

We are left with a great many questions with regards to conservation efforts and biodiversity survey data for Lesser Antillean bats. Many of these questions relate to how our survey data can be integrated into conservation and management decisions that impact a broad range of biodiversity. We have a great deal of work yet to do.

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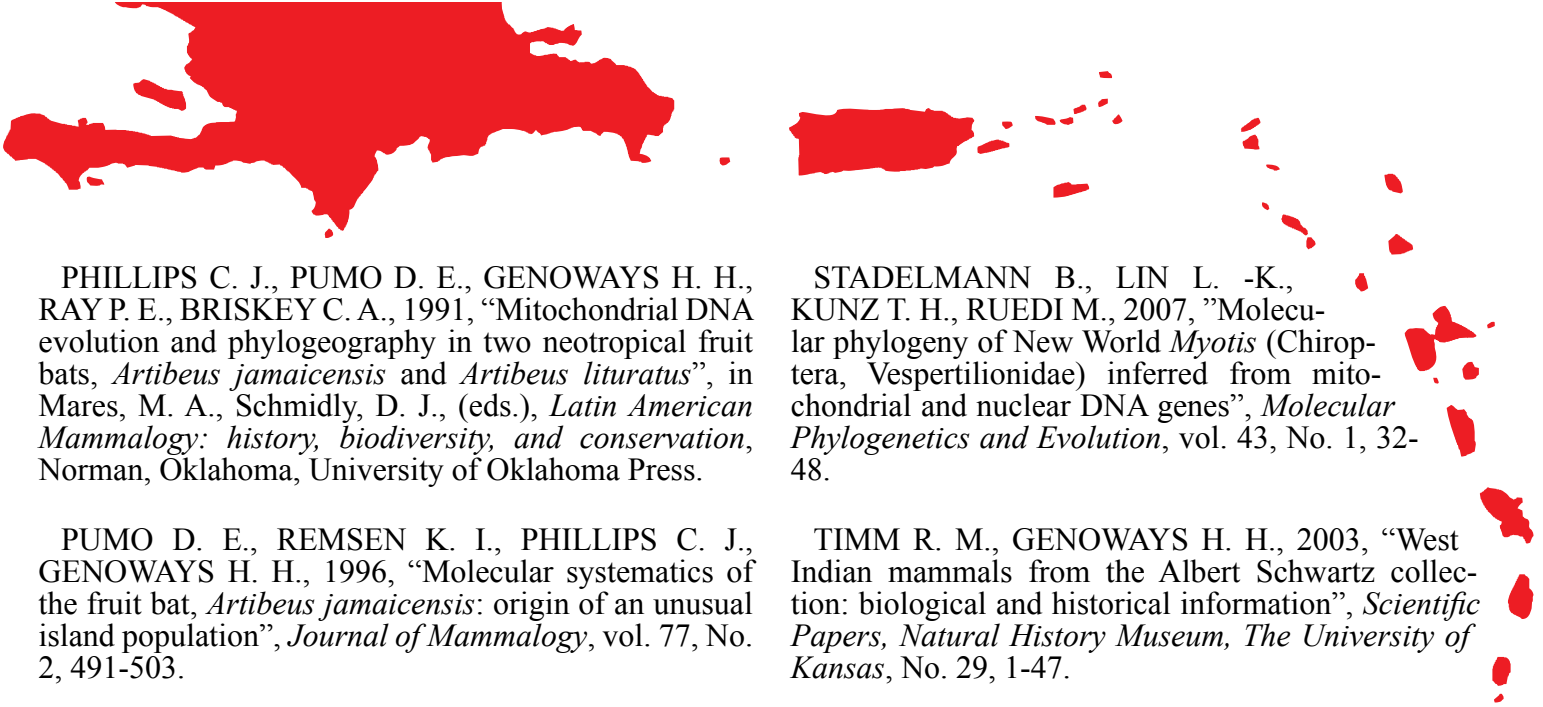
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